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Reef Faunal Response to Warming Middle U.S. Continental Shelf Waters*

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Abstract.—A North Carolina reef fish community was resurveyed with scuba gear to determine if changes occurred in community structure after 15 years of intense fishing. Generally, fishes important in the recreational and commercial fisheries were smaller, and large changes occurred in relative abundance and species composition. Indicative of a warming trend, total species composition of fishes had become more tropical, and a tropical sponge previously unrecorded at this latitude off the North Carolina coast became common. Two new (to the area) families and 29 new species of tropical fishes were recorded. Observations of 28 species of tropical reef fishes increased significantly. No new temperate species were observed, and the most abundant temperate species decreased by a factor of 22. Mean monthly bottom water temperatures in winter were 1–6°C warmer during the recent study. An increase in fish-cleaning symbiosis was especially noticeable. The study site is among the most northern permanent reef fish communities in the United States. Warmer bottom water temperatures along the subtidal continental shelf off Beaufort, North Carolina since 1977, have resulted in a dramatic increase in the tropical reef faunal composition. (Total species composition of fish became more tropical, and a tropical sponge previously unrecorded at this latitude became prominent.) Divers recorded two new (to the area) families and 29 new species of tropical fishes. Observations of 28 other species of tropical reef fishes increased significantly. No new temperate fishes were observed, and the most abundant temperate fish decreased 22-fold. Fishery landings data also showed a shift toward a more tropical reef fish community. (Mean monthly winter bottom water temperatures were 1-6°C warmer during the recent study.) This reef fish community paper along with two other demersal fauna papers indicate that thermal conditions of the oceans in general are changing and that both temperate and tropical components of the faunal communities are concurrently shifting toward a more tropical composition of species.

Introduction

Diver observations and tagging studies indicate that reef fish communities remain relatively stable (deterministic theory) in the absence of external stimuli (Beaumariage 1969; Smith and Tyler 1975; Smith 1978; Brock et al. 1979; Parker et al. 1979; Fable 1980; Gladfelter et al. 1980; Anderson et al. 1981; Parker 1990; Greene and Shenker 1993). However, some investigators have shown reef fish communities to be unstable (stochastic theory) (Sale 1977, 1978a, 1978b, 1980a, 1980b; Sale and Dybdahl 1978; Talbot et al. 1978). Instability has often been associated with microhabitats such as coral heads and small patch reefs and often involves differences in recruitment timing of juvenile reef fish.

Parker (1990) conducted an underwater reef fish survey between 1975 and 1977 to determine species composition of a typical inshore reef fish community in a northern latitude and described abundance of recreationally and commercially important fishes. In this study we examined changes that occurred in this community after 15 years of intense fishing by commercial and recreational fishers. We compared the results from two 3-year diving surveys and catch data from local headboats (i.e., recreational fishing vessels with passenger capacities of more than six anglers and with passage usually charged on a per person or per "head" basis). This study was motivated by an obvious decline in fish size and catch per unit of effort (CPUE) for some valuable species since 1975 (Huntsman et al. 1992; Parker and Mays 1998).

Methods

From 1990 to 1992 we repeated Parker's (1990) survey of rock outcroppings known by local fishermen as the "210 Rock." This reef was fished heavily during the 15

*An expansion and update of the global warming aspect of a 1998 published paper in the Transactions of the American Fisheries Society. "Changes in a North Carolina Reef Fish Community after 15 Years of Intense Fishing - Global Warming Implications" by R. O. Parker Jr. and R. L. Dixon. 127:908-920.

years separating the two surveys. Its 4-m maximum relief consists of bioeroded limestone and carbonate sandstone outcroppings (Newton et al. 1971) overgrown with sponges, hydroids, algae, soft corals, and diminutive hard corals separated by valleys of sand and broken shell. The ledges are located 44 km south of Beaufort Inlet, North Carolina (348149N, 768359W) in depths of 27–33 m (Figure 1). Observations and counts of fishes were made during scuba dives on Parker's (1990) station (marked by an underwater buoy on top of a 2-m ledge); we also surveyed five additional stations to increase sample size. Because of limited bottom time (17 minutes breathing compressed air, 5 minutes to find the station, and a 3-minute safety margin), only fishes important in the recreational and commercial fisheries were counted. Time was allocated for three dives per month, but adverse weather, lost surface buoys, or problems with the support vessel precluded some dives. In the initial survey, counts were made during 48 dives from October 1975 to March 1980; sampling effort was extended beyond the three-year study period to obtain more data in winter months. In our repeat survey, we conducted 31 dives from April 1990 to July 1993 (Table 1). The senior author made most of the fish counts on the primary station during both survey pe-

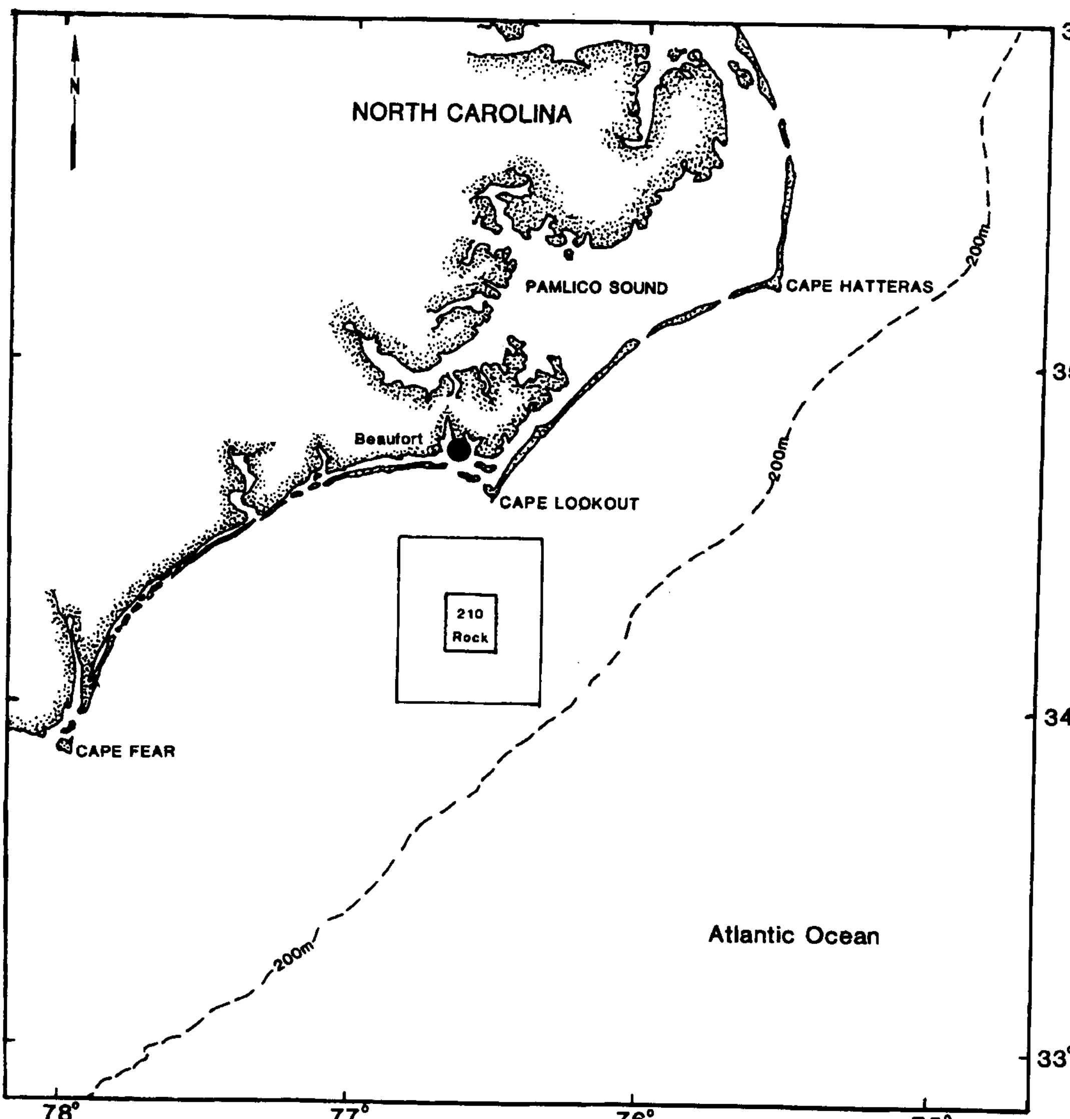

Figure 1. The 210 Rock is 44 km south of Beaufort Inlet in depths of 27–33 m. Only catch and effort data from 210 Rock study site and the surrounding area (delineated by the outer square) were used in the analyses.

Table 1. Number of dives per month that included counts of fishes important in the recreational and commercial fisheries.

Month	Initial survey (Parker 1990)							Recent survey				
	1975	1976	1977	1978	1979	1980	Total	1990	1991	1992	1993	Total
Jan			2		2		4					
Feb						1	1		1			1
Mar		1	1		2	1	5			1		1
Apr		2	1				3	1				1
May		1	1	1	1		4		1	1	2	4
Jun		1	1	2	3		7	1		1	1	3
Jul		1	1	3			5		1	1	1	3
Aug		1		5			6	3	3	1		7
Sep			2	1			3	2	2			4
Oct	1	1	1	1			4		1	1		2
Nov	2	2	1				5	3	1	1		5
Dec			1				1					
Total	3	10	12	13	8	2	48	10	10	7	4	31

riods, and the junior author conducted most of the fish surveys of the additional stations. Fish counts at only the primary station were compared between the two surveys, whereas total fish species composition on all dives was compared between the surveys.

We used the Wilcoxon two-sample test (nonparametric comparisons) to test the hypothesis of no difference in tropical species frequency of occurrence between the two study periods (a50.05). Frequency of occurrence data were adjusted by differences in sampling effort among years and sorted in descending order in the first study and ascending order in the second to show temporal groups.

We based our definitions of tropical and temperate species on the ranges of fishes given in Robins et al. (1986), tropical species being common to the Caribbean, Bahamian, and south Florida banks and temperate species being common north of Cape Hatteras.

Bottom water temperature and secchi disk (30 cm in diameter) readings were taken during the first dive after recording counts and behavior of fishes. Bottom water temperatures were recorded from a hand-held thermometer during both studies and a temperature data logger during the recent study. Lateral secchi disk measurement was used to estimate radius visibility for 3608 at each station; 75% of the distance measured was used to calculate sample area because fishes fade from view beyond that (Parker 1990). Dives were scheduled near the time of full moon, when many reef fishes spawn (Colin et al. 1987; Gilmore and Jones 1992). In addition to counting fish, divers recorded conspicuous fish behavior such as spawning, feeding activities, cleaning symbiosis, and defense of territories.

Catch and fishing effort (in angler days, defined as one angler fishing aboard a headboat with a rod and reel for about six hours, excluding transit time) by species for the headboat fishery were calculated from catch reports submitted by vessel personnel as part of the U.S. South Atlantic Headboat Survey during 1975–1977 (Dixon and Huntsman, in press) and 1990–1992 (Dixon et al., unpublished data). Catch and effort data from nine statistical reporting grids (16 × 16 km each), adjacent to and inclusive of the 210 Rock were used in the analyses. Mean weights by species were calculated from individual fish weights collected during dockside sampling of headboat landings.

Results

Abundance

As indicated by headboat survey data and underwater observations, fishes important in the recreational and commercial fisheries were generally smaller in the recent study, and large changes in relative abundance and species composition were apparent. Total species composition of fishes shifted toward a more tropical assemblage (Appendix), and a tropical sponge previously unrecorded at this latitude off the North Carolina coast became prominent.

Although commercial landings of reef fishes and headboat fishing effort in North Carolina had increased since 1977 (Figure 2), the mean weights of 15 of the 20 target species (economically important) declined (Table 4). The CPUE in number of fish increased for most target species; exceptions were red porgy, red snapper, black sea bass, and greater amberjack (Table 4). The increase in reported landings of bank sea bass is misleading because earlier catches, although recognized by headboat personnel as a different species, were reported as black sea bass. Also, during 1975–1977, some almaco jacks might have been reported as greater amberjacks. Some tropical species that were previously rare or absent during the 1975–1977 headboat catches from 210

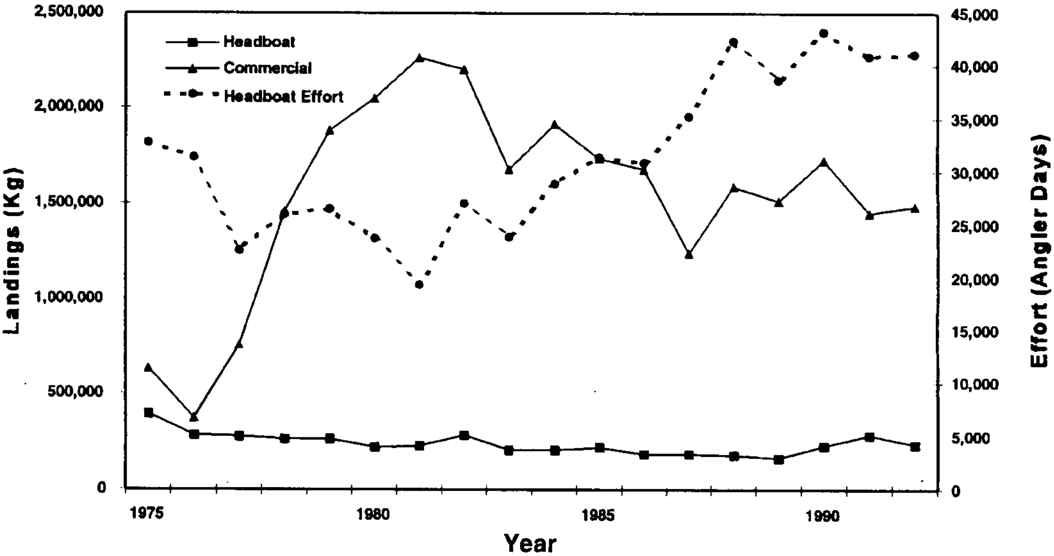

Figure 2. Landings of reef fishes for the North Carolina headboat and commercial fisheries and fishing effort for the North Carolina headboat fishery, 1975–1992.

Rock and the surrounding area were landed more frequently during 1990–1992 (Table 5).

Sea basses were the most abundant predators we observed while diving on 210 Rock, and scamps surpassed gags as the most predominant sea bass. Visual estimates in the initial survey were 673 gags/ha and 30 scamps/ha; recent visual estimates were 204 gags/ha and 300 scamps/ha (see Table 6 for species abundance and density data). The frequency of occurrence of red grouper increased more than fivefold, from 6% to 32% (see Appendix for frequency data) and four previously unrecorded species of sea bass were observed: yellowmouth grouper, rock hind, red hind, and graysby. Yellowmouth grouper, which ranged from 200 to 500 mm long, were seen eight times (bicolor phase only, probably because the uniform coloration of this species is difficult to distinguish from that of the scamp underwater). The frequency of occurrence of bank sea bass increased slightly from 92% to 96%, but black sea bass (the most abundant temperate species) decreased from 92% to 68%. Visual estimates of black sea bass decreased by a factor of 22, from 1,554 to 70 fish/ha.

Snappers were much less frequently observed than sea basses. Snappers in general, and vermilion snapper in particular, tended to avoid divers; when sightings occurred, they were fleeting. Vermilion snapper are mesopelagic feeders (Dixon 1975) and, thus, could be missed by divers concentrating on bottom fishes. Densities of red snapper and vermilion snapper both decreased from 32 and 785 fish/ha, respectively, to 0 fish/ha. Schoolmasters were seen for the first time in November 1990 and again in February 1991.

We observed only two species of grunts while diving at 210 Rock and both are permanent residents. The frequency of occurrence of the white grunt increased slightly (94–97%), but its density increased nearly twofold from 246 to 414 fish/ha. Tomtates increased in frequency of occurrence from 65% to 84% but decreased in density from an estimated 41,934 to 17,111 fish/ha. Estimates of tomtates were highly variable because of the presence and absence of large schools, which sometimes included thousands of juveniles.

The two most abundant porgies at 210 Rock were observed less frequently in the recent study: occurrence of red porgy decreased from 60% to 45% and spottail pinfish decreased from 71% to 45%. Density of red porgy decreased from 254 to 33 fish/ha. The frequency of occurrence of knobbed porgy increased almost fourfold, from 25% to 97%.

Hogfish, caught both recreationally and commercially, were seen for the first time in the recent study. They were observed during 77% of the dives.

Round scad, one of the primary food sources for large reef fishes, decreased in frequency of occurrence from 54% to 16% and in density from 16,795 to 3,017 fish/ha. Like the tomtate, round scad estimates were highly variable due to the presence and absence of large schools, which sometimes included thousands of individuals.

Twenty-nine tropical fishes were recorded for the first time, and 27 other tropical fishes increased more than twofold in frequency of occurrence during the 1990–1993

Table 2. Changes in the assemblage (by frequency of observation) of tropical fishes at 210 Rock off Beaufort, North Carolina, between the 1975–1980 and 1990–1993 surveys. Observation category is based on the number of dives on which a species was observed (rare, ≤5 dives; occasional, 6–10 dives; comon, 11–20 dives; and abundant, >20 dives); N = number of species.

		Number of species that:			
Observation category	Number of new species (%)	Increased substantially[a] (%)	Decreased substantially[b] (%)	Vanished (%)	Changed slightly[c] (%)
Rare (29)	16 (55)	1 (3)	0 (0)	9 (31)	3(10)
Occasional (14)	6 (43)	5 (36)	1 (7)	2 (14)	0 (0)
Common (19)	5 (26)	10 (53)	1 (5)	0 (0)	3 (16)
Abundant (28)	2 (7)	11 (39)	0 (0)	0 (0)	15 (54)
Total (90)	29 (32)	27 (30)	2 (2)	11 (12)	21 (23)

a. More than twofold (Table 3 lists species that increased *significantly*, $P \leq 0.05$)
b. More than 50%
c. Less than a factor of 2

study, whereas only two tropical fishes decreased by more than 50% (Table 2). Eleven tropical fishes recorded previously were not observed during the recent study. Thus, there was a net increase in occurrence for 43 tropical fish species, 28 of which increased significantly ($P = 0.05$; Table 3). Occurrences of new tropical species and those with increased occurrences in the recent study were represented in all four observation categories: rare, occasional, common, and abundant (Table 2).

The *Scaridae* (parrotfishes) was a conspicuous new family of reef fishes on 210 Rock. Although parrotfishes were not recorded during the earlier study, one juvenile parrotfish *Sparisoma* spp. was photographed in 1975 with other reef fishes at a cleaning station on 210 Rock (Parker and Ross 1986). Two juvenile stoplight parrotfish were seen in the recent study, and one about 120 mm in total length was photographed. This is a northern latitude distribution record (S. W. Ross, Center for Marine Science Research, personal communication), but the absence of adults indicates that this species does not spawn in the study area.

Three unidentified species were observed for the first time in the recent study: a mojarra (another family of reef fishes new to the study area), a toad- fish, and a boxfish. The boxfish was a young of the year, about 30 mm long × 20 mm wide × 20 mm high, with alternate black and yellow 5-mm markings. Other species, not previously mentioned, observed for the first time were (in order from the most to least frequently encountered) doctorfish, bigeye, squirrelfish, night sergeant, trumpetfish, inshore lizardfish, banded butterfly- fish, glasseye snapper, sharptail eel, tattler, creole wrasse, goby, red cornetfish, and scrawled filefish. In addition, butter hamlet in five color phases (butter, barred, indigo, blue, and yellowbelly) and two new species of angelfish, rock beauty and French angelfish, were observed for the first time.

Many species increased threefold or more. The blue angelfish and queen angelfish increased about 3-fold and 16-fold, respectively (Appendix). Other species that exhibited increases of this magnitude include spotted goatfish (26-fold), yellow goatfish (13-fold), spotfin butterflyfish (3-fold), reef butterflyfish (10-fold), sunshinefish (21-fold), blue chromis (3-fold), dusky damselfish (5-fold), spot- fin hogfish (5-fold), bluehead (3-fold), ocean surgeon (3-fold), blue tang (13-fold), and bandtail puffer (11-fold).

No new temperate fishes were recorded during the recent study. Pelagic species (e.g., sharks, jacks, and mackerel) were recorded, but they were not the focus of this study. The basket sponge, also a tropical species, was recorded for the first time during the recent study and appeared to be abundant, although density was not estimated (Appendix). This species was previously recorded only as far north as Cape Fear, North Carolina, 96 km south of our study site. A report by the South Carolina Wildlife and Marine Resources Department and Duke University Marine Laboratory (SCWMRD and DUML 1982) also supports the absence of basket in the vicinity of 210 Rock during our earlier survey.

Temperature

Mean monthly bottom water temperatures were warmer by 1–68°C from January through March and slightly cooler (1.78°C) from April through December during the recent study (Figure 3). Bottom water temperatures during January through March in the recent survey ranged from 11.98°C (18 March 1993) to 22.78°C (30 March 1993; A. Powell, National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort Laboratory, unpublished data) compared with 5.78°C (9 February 1977) to 19.48°C (26 March 1976) in the earlier survey. Bottom water temperatures during April through Decem-

Table 3. Frequency of occurrence (in proportion of dives each year) of tropical fish species observed during only one of the two surveys or, if observed during both surveys, that increased significantly ($P \leq 0.05$) in frequency between surveys at 210 Rock off Beaufort, North Carolina. Species are sorted in descending order in the initial survey and ascending order in the recent survey according to their adjusted frequency of occurrence by year, thus delineating warmer winter tropical groups. See Table 1 for number of dives each year.*

	Initial survey (Parker 1990)						Recent survey			
Species	1975	1976	1977	1978	1979	1980	1990	1991	1992	1993
Scamp*	1.0	0.8	0.1	0.3	0.5		0.9	1.0	1.0	1.0
Cocoa damselfish*	1.0	0.7	0.3	0.2	0.4		0.9	1.0	0.7	0.8
Spanish hogfish*	0.3	0.3	0.4	0.2	0.3	0.5	0.6	0.9	1.0	1.0
Spotfin hogfish*		0.4	0.2	0.1		0.5	0.9	0.9	1.0	1.0
Bluehead*	0.3		0.4	0.3			1.0	1.0	0.9	1.0
Knobbed porgy*		0.3	0.4	0.3			1.0	1.0	0.9	1.0
Spotfin butterflyfish*		0.5	0.3	0.1			0.7	0.6	0.7	1.0
Longspine porgy			0.1	0.3	0.4					
Vermilion snapper		0.3	0.1		0.4					
Conger spp. eel			0.1		0.1	0.5				
Spotted drum	0.7									
Bandtail puffer*	0.3	0.2					0.7	1.0	0.6	0.3
Sea chub	0.3	0.1								
Yellowtail damselfish	0.3									
Reticulate moray		0.2	0.1							
Dusky damselfish*		0.2	0.1				0.3	0.1	0.4	1.0
Crested blenny					0.3					
Queen angelfish*		0.2					0.8	0.5	0.7	0.8
Reef butterflyfish*			0.2				0.3	0.3	0.7	0.5
Honeycomb moray					0.1					
Puffer			0.1							
Sand perch*			0.1				0.3	0.1	0.1	0.3
Spotted goatfish*				0.1			0.5	0.8	0.4	0.3
Mojarra							0.1			
Scrawled filefish								0.1		
Toadfish									0.1	
Boxfish									0.1	
Stoplight parrotfish							0.2			
Schoolmaster							0.1	0.1		
Rock beauty							0.1	0.1		
Red cornetfish							0.1		0.1	
Sharptail eel								0.1	0.1	
Red hind									0.3	
Creole wrasse*							0.1	0.1	0.1	
Glasseye snapper								0.1	0.3	
Tattler*								0.1	0.1	0.3
French angelfish*								0.2	0.1	0.3
Graysby*							0.1	0.1	0.4	
Banded butterflyfish								0.4	0.3	
Trumpetfish*							0.2	0.3	0.3	
Night sergeant*							0.4	0.4	0.1	
Inshore lizardfish*								0.1	0.4	0.5
Squirrelfish								0.5	0.7	
Scarus spp. parrotfish*							0.1	0.7	0.4	
Butter hamlet*							0.2	0.6	0.4	
Yellowmouth grouper*							0.1	0.1	0.6	0.5
Sparisoma spp. parrotfish*							0.1	0.6	0.4	0.3
Rock hind*							0.2	0.5	0.6	0.5
Bigeye*							0.5	0.6	0.7	0.5
Doctorfish*							0.6	0.9	0.9	
Hogfish*							0.6	0.9	0.9	0.8

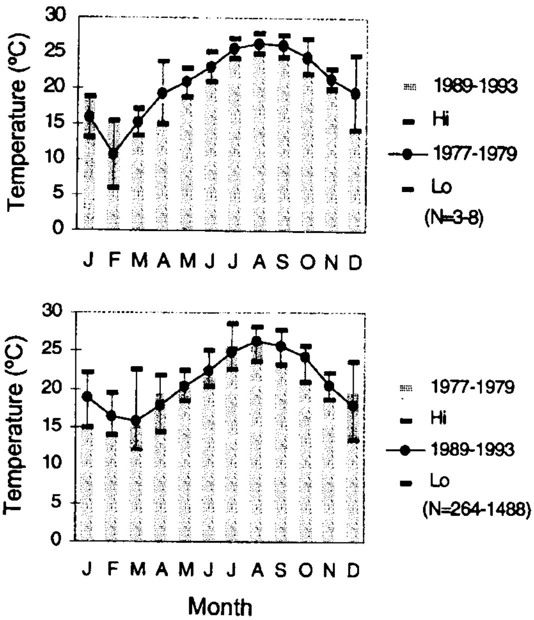

Figure 3. Mean monthly (January–December) bottom water temperatures at 210 Rock south of Beaufort Inlet, North Carolina; *N* = monthly records; bars indicate the range of temperatures). (Top) Early survey data (black dots) are shown overlaying recent data (gray bars). (Bottom) Recent survey data (black dots) overlay data from earlier survey (gray bars).

ber ranged from 14.38°C in December to 28.58°C in August recently (Powell, unpublished data) compared with 16.38°C in December to 28.08°C in August formerly.

In the 1975–1977 study, two successive years of extremely low bottom water temperatures were recorded: 7.88°C on 5 February 1976 and 5.78°C on 9 February 1977. The only other bottom water temperature recorded in February during this period was 138°C on 25 February 1976. In the recent survey, February daily bottom water temperatures ranged from 14.28°C to 18.98°C, and no extreme lows occurred during the 1991–1993 period (Powell, unpublished data). These data suggest a major shift to warmer bottom water temperatures in winter.

Discussion

Although our study was undertaken to record the in situ effects of 15 years of intense fishing on a North Carolina reef fish community, we found that changes associated with environmental factors confounded that objective and were more dramatic. Dockside samples and catch records showed that, generally, average weights of economically important fishes were smaller but that landings by weight increased because fishing effort increased. Our underwater observations supported smaller average sizes of target species, but they also indicated large changes in relative abundance and a major increase in tropical species.

Headboat landings and CPUE increased for tropical fish species (Table 5) usually associated with reefs off Florida, the Bahamas, and the Caribbean islands and decreased substantially for black sea bass, a temperate species. Although increased fishing effort could cause the decline in black sea bass populations, this does not explain the increase in the more tropical species. In the early and mid-1970s, these tropical species (lane snapper, red hind, yellowfin grouper, squirrelfish, short bigeye, coney Epinephelus fulvus, queen triggerfish, bigeye, hogfish, and trumpetfish) were reported in headboat landings from the Cape Fear, North Carolina, area but were rarely caught north of 348N latitude. Headboat personnel are known for their interest in rare or unusual species and would have recorded them on catch logs or contacted a port agent for identification.

Behavioral observations support tropical fishes establishing residency rather than simply passing through. A spawning ritual of hogfish was observed 7 May 1993, and at least 12 species of young-of-the-year reef fishes were seen during our two surveys. At least nine species of young-ofthe- year reef fishes were seen during the recent survey, whereas seven species were seen earlier (Table 7). Cleaning symbiosis involving wrasses and gobies was observed on seven occasions during the recent study but only on three occasions previously, when water temperatures were above 20°C.

In September 1995, the United Nations sponsored an Intergovernmental Panel on Climate Change, which unofficially concluded that there is a 90% or better chance that global warming had begun (Kerr 1995). Global warming has been implicated by long-term global changes in atmospheric conditions: for example, CO_2 increase from 200 (World Meteorological Organization 1990) and 160,000 (Barnola et al. 1987) years of data and surface air warming from 100 years of data (World Meteorological Organization 1990; Hansen and Lebedeff 1987).

Warmer water is affecting marine ecosystems. Global sea-surface temperature maps show that coral reef bleaching episodes between 1983 and 1991 followed warm-season hot spots (i.e., 18°C above long-term monthly averages; Goreau and Hayes 1994). Recent marine species range extensions also have been related to warmer water temperatures. Barry et al. (1995) related climate warming between 1931 and 1994 to northward shifts in invertebrate ranges in a California rocky intertidal community: abundance for eight of nine southern species increased and five of eight northern species decreased. Murawski (1993) examined bottom-trawl surveys of the northwest Atlantic Ocean between 1967 and 1990 and associated statistically significant poleward

Table 4. Changes in reported catch, catch per unit effort (CPUE), and mean weight (± SE) of target species between the 1975–1977 period and the 1990–1992 period for the headboat fishery in the 210 Rock area; N = sample size.

Species	Number landed	CPUE	Mean weight (kg)	*N*	Number landed	CPUE	Mean weight (kg)	*N*
Red porgy	12,157	2.42	1.10 ± 0.01	1,455	13,423	1.72	0.51 ± 0.01	1,386
Whitebone porgy	423	0.08	0.71 ± 0.04	45	665	0.09	0.52 ± 0.02	136
Knobbed porgy	32	0.01	1.08 ± 0.07	39	1912	0.25	0.64 ± 0.02	223
Spottail pinfish	555	0.11	0.52 ± 0.02	92	11,296	1.45	0.30 ± 0.00	1,212
Vermilion snapper	8,563	1.70	1.00 ± 0.02	747	30,634	3.94	0.40 ± 0.01	1,764
Red snapper	94	0.02	5.09 ± 0.28	126	129	0.02	2.36 ± 0.29	41
Red grouper	7	0.00	4.20 ± 0.91	20	98	0.01	2.93 ± 0.26	42
Rock hind	3	0.00	1.03 ± 0.09	8	99	0.01	0.61 ± 0.05	26
Graysby			0.36	1	217	0.03	0.41 ± 0.04	9
Gag	830	0.16	5.71 ± 0.25	286	2,330	0.30	2.85 ± 0.09	308
Scamp	267	0.05	3.28 ± 0.33	84	1,166	0.15	1.12 ± 0.07	263
Black sea bass[a]	30,404	6.04	0.44 ± 0.01	538	6,995	0.90	0.33 ± 0.02	845
Bank sea bass[a]			0.14 ± 0.01	40	3,185	0.41	0.24 ± 0.03	194
White grunt	7,167	1.42	0.71 ± 0.01	904	16,476	2.12	0.43 ± 0.00	2,042
Tomtate	167	0.03	0.19 ± 0.01	30	9,163	1.18	0.21 ± 0.00	488
Gray triggerfish	2,627	0.52	2.3 ± 0.05	211	6,373	0.82	1.22 ± 0.03	500
Greater amberjack[b]	309	0.06	9.77 ± 0.86	63	454	0.06	8.71 ± 0.80	41
Almaco jack[b]			6.75 ± 0.49	42	138	0.02	5.81 ± 0.51	54
King mackerel					308	0.04	3.48 ± 0.29	30
Little tunny					78	0.01	4.18 ± 0.44	8

a. During 1975–1977, headboat personnel reported catches of bank sea bass as black sea bass, so 1975–1977 catches of bank sea bass were actually higher than reported and black sea bass catches were lower.
b. During 1975–1977, headboat personnel probably reported almaco jacks as greater amberjacks, thereby inflating greater amberjack catches and deflating almaco jack catches.

range extensions of two pelagic and five demersal fish species with warmer (18°C) water temperatures.

Although intrusion of deeper, cold (21.0–22.58°C) Gulf Stream water into Onslow Bay (where 210 Rock is located) during the summer has been reported (Blanton 1971; Stefansson et al. 1971; Blanton and Pietrafesa 1978; and Hofmann et al. 1981), no severe winter cold water (88°C) intrusions have been documented. Mathews and Pashuk (1984) summarized water temperature data from 1940 to 1981 between Cape Fear, North Carolina (96 km south of our study site), and Cape Canaveral, Florida. They found that 1963, 1977, and 1978 were the coldest

Table 5. Changes in reported catch, catch per unit effort (CPUE), and mean weight (6SE) of tropical fish species that were absent or rare during the 1975–1977 surveys and that significantly increased in numbers landed between the 1975–1977 survey and the 1990–1992 survey of the 210 Rock area; N = sample size.

	1975–1977				1990–1992			
Species	Number landed	CPUE	Mean weight (kg)	*N*	Number landed	CPUE	Mean weight (kg)	*N*
Lane snapper								
Lutjanus synagris					100	0.0128		
Gray snapper								
L. griseus					1	0.0001		
Red hind	4	0.0008	0.95 ± 0.12	9	39	0.0050	0.82 ± 0.08	22
Yellowfin grouper								
Mycteroperoa venenosa					1	0.0001	1.00 ± 0.44	5
Queen triggerfish								
Balistes vetula	1	0.0002			108	0.0139	1.00 ± 0.20	3
Squirrelfish	6	0.0012	0.39 ± 0.16	2	76	0.0098	0.39 ± 0.03	4
Short bigeye								
Pristigenys alta					30	0.0038	0.42 ± 0.04	7
Bigeye					538	0.0691	0.86 ± 0.04	37
Trumpetfish					1	0.0001		
Hogfish					3	0.0004	5.30	1

Table 6. Visual estimates of abundance of prominent species at 210 Rock important in the recreational and commercial fisheries off Beaufort, North Carolina; N = number of counts.

	1975–19780			1990–1993		
Species	Total fish (N = 48)[a]	Fish/ha (N = 33–48)[b]	95% Confidence interval (fish/ha)	Total fish (N = 31)[a]	Fish/ha (N = 21–28)[b]	95% Confidence interval (fish/ha)
Gag	800	673	328–1,018	116	204	29–379
Scamp	57	30	10–50	293	300	136–464
Black sea bass	898	1,554	440–2,668	52	70	10–130
Red snapper	70	32	10–54	0		
Vermilion snapper	1,063	785	0–2,113	0		
Red porgy	193	254	0–527	22	33	0–72
White grunt	329	246	113–378	212	414	0–851
Tomtate	24,666[d]	41,934	0–86,501	26,287[e]	17,111	2,618–3,1604
Round scad	24,700[f]	16,795	1,766–31,824	10,000[g]	3,017	0–9,310

a. Includes counts in unmeasured visibility.
b. Some counts are less than "total" N because fishes observed on some dives but not counted could not be averaged; thus the entire record for some dives had to be omitted from the analysis.
c. 2,309 Black sea bass/ha; 5 February–9 July 1976 comparison.
d. Counts = 36 with 15 in the 100s; 8 counts in 100s at the same time round scad counts were in 100s.
e. Counts = 19 (seen 28 times total).
f. Counts = 40 with 13 in the 100s; 8 counts in 100s at the same time tomtate counts were in 100s.
g. Counts = 2 (seen four times total).

(8.58°C) winters on record in South Carolina coastal waters (18 m deep). In a summary of additional data, Mathews and Pashuk (1986) found that from 1973 to 1979, the winter bottom (28–55 m) water temperatures remained above 10.38°C. Thus, it appears that our winter bottom water temperature data are unique to our study site location, depth, and time.

Our results indicate that increases in abundance and numbers of reef species toward a more tropical community were most likely due to warmer winter bottom water temperatures. Twenty-nine tropical fishes and the basket sponge, first recorded at the study site during the recent survey, were not observed prior to the extreme low recordings of bottom water temperatures in February of 1976 and 1977. Overall, 28 species of tropical reef fishes increased significantly during the recent survey. Spring, summer, and fall bottom water temperatures were similar during the two surveys (Figure 3).

Table 7. Approximate numbers of young-of-year fishes observed during June 1976–July 1978 and during August 1990–July 1992 and corresponding bottom water temperatures (temp).

Survey period and date	Tomtate	Purple reeffish	Yellowtail reeffish	Spottail pinfish	Sea basses	Snappers	Blue chromis	Bluehead	Unknown jacks	Others	Temp (C°)
1976–1978											
24 Jun 1976						1,000s					
17 May 1977			2	1,000s							21.5
17 May 1978										1,000s	20.8
31 May 1978	100s	100s									21.0
12 Jun 1978		> 50									20.3
21 Jun 1978		> 24	1								20.8
13 Jul 1978		> 24	6								27.0
1990–1992											
3 Aug 1990							> 24				
23 Aug 1990										1,000s	28.6
27 Nov 1990	100								50[a]		21.4
30 May 1991	1,000s	> 50	> 24								26.0
5 Sep 1991								> 24			28.9
16 Sep 1991										1[b]	27.2
30 Jul 1992										1[c]	26.2

a All observed around a surface buoy.
b One scamp (approximately 60 mm).
c One bigeye (approximately 25 mm) seen around a surface buoy.

Although more stations were surveyed during the recent study (6 versus 1), fewer dives (total effort) were made. The additional stations (to search for more species and to observe fish behavior, as time permitted) were along a ledge that was included in the initial survey. Thus, the dramatic increase in tropical species during the recent survey appears unrelated to differences in sampling effort.

We observed fewer piscivorous fishes in the recent survey, but the reduction probably had little to do with the proliferation of tropical fishes in the area. Our estimated abundance of eight piscivorous species (excluding round scad—not a piscivore; Table 6) at 210 Rock decreased for six species from an aggregate 45,508 to 18,132 fish/ha; however, CPUE by headboat anglers increased in the study area for 13 of 16 piscivorous fishes (excluding pelagic fishes like jacks and mackerels; Table 4). Thus, change to a more tropical faunal composition can be reasonably explained only by the absence of severely low water temperatures. Our subtidal reef fish study, the northwest Atlantic Ocean subtidal demersal and pelagic fish study by Murawski (1993), and the California intertidal invertebrate study by Barry et al. (1995) all indicate that bottom water temperatures along the northern U.S. continental shelf are warming, that thermal conditions of the oceans in general are changing, and that previously both temperate and tropical faunal communities are concurrently shifting toward a more tropical composition of species.

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Appendix: Frequency Data for Observed Species

Number (and percent) of scuba dives on 210 Rock near Beaufort, North Carolina, during which fish and sponge species were observed (= frequency of occurrence) during October 1975–March 1980 and April 1990–August 1993 (48 and 31 dives, respectively). Fish species are listed by Family in the same order as in Robins et al. (1991).

Taxona	Number (%) during: 1975–1980[b]	1990–1993
Fish		
Rhincodontidae		
Ginglymostoma cirratum nurse shark	2 (4.2)	
Odontaspididae		
Odontaspis taurus sand tiger	1 (2.1)	
Carcharhinidae		
Carcharhinus leucas bull shark	1 (2.1)	
C. obscurus dusky shark		1 (3.2)
Galeocerdo cuvier tiger shark	1 (2.1)	
Rhizoprionodon terraenovae Atlantic sharpnose shark	5 (10.4)	
Sphyrnidae		

Taxona	Number (%) during: 1975–1980[b]	1990–1993
Sphyrna spp. hammerhead	1 (2.1)	
Dasyatidae		
Dasyatis spp. stingray	3 (6.3)	2 (6.5)
Muraenidae		
Gymnothorax moringa spotted moray (S)	5 (10.4)	5 (16.1)
G. saxicola honeycomb moray (S)	1 (2.1)	
Muraena retifera reticulate moray (S)	3 (6.3)	
Ophichthidae		
Myrichthys breviceps sharptail eel (S)		4 (12.9)
Congridae		
Conger spp. eel[c] (S)	3 (6.3)	
Clupeidae		
Sardinella aurita Spanish sardine	2 (4.2)	
Synodontidae		
Synodus foetens inshore lizardfish (S)		6 (19.4)
Gadidae		
Urophycis earlli Carolina hake (S)	9 (18.8)	2 (6.5)
Batrachoididae		
Opsanus spp. toadfish[d] (S)		1 (3.2)
Lophiidae		
Lophius americanus goosefish (N)	1 (2.1)	
Holocentridae		
Holocentrus adscensionis squirrelfish (S)		10 (32.3)
Aulostomidae		
Aulostomus maculatus trumpetfish (S)		7 (22.6)
Fistulariidae		
Fistularia petimba red cornetfish (S)		2 (6.5)
Scorpaenidae		
Scorpaena dispar hunchback scorpionfish (S)	1 (2.1)	
Serranidae		
**Centropristis ocyurus* bank sea bass (S)	44 (91.7)	30 (96.8)
**C. striata* black sea bass (N)	44 (91.7)	21 (67.7)
Diplectrum formosum sand perch (S)	1 (2.1)	6 (19.4)
**Epinephelus adscensionis* rock hind (S)		13 (41.9)
**E. cruentatus* graysby (S)		5 (16.1)
**E. morio* red grouper (S)	3 (6.3)	10 (32.3)
**E. guttatus* red hind (S)		2 (6.5)
Hypoplectrus unicolor butter hamlet (S)		20 (64.5)
Liopropoma eukrines wrasse bass (S)	9 (18.8)	20 (64.5)
**Mycteroperca interstitialis* yellowmouth grouper (S)		8 (25.8)
**M. microlepis* gag (S)	48 (100.0)	30 (96.8)
**M. phenax* scamp (S)	20 (41.7)	30 (96.8)
Rypticus maculatus whitespotted soapfish (S)	29 (60.4)	21 (67.7)
Serranus phoebe tattler (S)		3 (9.7)
S. subligarius belted sandfish (S)	41 (85.4)	23 (74.2)
S. tigrinus harlequin bass (S)	3 (6.3)	17 (54.8)
Priacanthidae		
Priacanthus arenatus bigeye (S)		18 (58.1)
P. cruentatus glasseye snapper (S)		3 (9.7)
Apogonidae		
Apogon pseudomaculatus twospot cardinalfish (S)	24 (50.0)	15 (48.4)
Rachycentridae		
Rachycentron canadum cobia		2 (6.5)
Echeneidae		
Remora remora remora		1 (3.2)
Carangidae		
Caranx bartholomaei yellow jack		5 (16.1)
C. crysos blue runner	4 (8.3)	
C. ruber bar jack	2 (4.2)	11 (35.5)
Decapterus punctatus round scad	26 (54.2)	5 (16.1)
**Seriola dumerili* greater amberjack	41 (85.4)	28 (90.3)
**S. rivoliana* almaco jack	7 (14.6)	11 (35.5)
S. zonata banded rudderfish		4 (12.9)
Coryphaenidae		
Coryphaena hippurus dolphin		2 (6.5)
Lutjanidae		
**Lutjanus apodus* schoolmaster (S)		2 (6.5)
**L. campechanus* red snapper (S)	17 (35.4)	1 (3.2)
**Rhomboplites aurorubens* vermilion snapper (S)	7 (14.6)	
Gerreidae		
Unidentified mojarra		1 (3.2)
Haemulidae		
**Haemulon aurolineatum* tomtate (S)	31 (64.6)	26 (83.9)
**H. plumieri* white grunt (S)	45 (93.8)	30 (96.8)
Sparidae		
**Archosargus probatocephalus* sheepshead (N)	2 (4.2)	
**Calamus leucosteus* whitebone porgy (S)	25 (52.1)	18 (58.1)
**C. nodosus* knobbed porgy (S)	12 (25.0)	30 (96.8)
**Diplodus holbrooki* spottail pinfsh (S)	34 (70.8)	14 (45.2)
**Pagrus pagrus* red porgy (S)	29 (60.4)	14 (45.2)
Stenotomus caprinus longspine porgy (S)	8 (16.7)	
Sciaenidae		
Equetus lanceolatus jackknife-fish (S)	5 (10.4)	11 (35.5)
E. punctatus spotted drum (S)	2 (4.2)	
E. umbrosus cubbyu (S)	39 (81.3)	27 (87.1)
Mullidae		
Mulloidichthys martinicus yellow goatfish (S)	1 (2.1)	9 (29.0)
Pseudupeneus maculatus spotted goatfish (S)	1 (2.1)	17 (54.8)
Kyphosidae		
Kyphosus spp. sea chub (S)	2 (4.2)	
Ephippidae		
Chaetodipterus faber Atlantic spadefish	6 (12.5)	9 (29.0)
Chaetodontidae		
Chaetodon ocellatus		

Taxona	Number (%) during: 1975–1980[b]	1990–1993
spotfin butterflyfish (S)	9 (18.8)	22 (71.0)
C. sedentarius reef butterflyfish (S)	2 (4.2)	13 (41.9)
C. striatus banded butterflyfish (S)		6 (19.4)
Pomacanthidae		
Holacanthus bermudensis		
blue angelfish (S)	16 (33.3)	30 (96.8)
H. ciliaris queen angelfish (S)	2 (4.2)	21 (67.7)
H. tricolor rock beauty (S)		2 (6.5)
Pomacanthus paru		
French angelfish (S)		4 (12.9)
Pomacentridae		
Abudefduf taurus night sergeant (S)		9 (29.0)
Chromis cyanea blue chromis (S)	3 (6.3)	7 (22.6)
C. enchrysurus		
yellowtail reeffish (S)	36 (75.0)	25 (80.6)
C. insolata sunshinefish (S)	1 (2.1)	14 (45.2)
C. multilineata brown chromis (S)	1 (2.1)	1 (3.2)
C. scotti purple reeffish (S)	45 (93.8)	29 (93.5)
Microspathodon chrysurus		
yellowtail damselfish (S)	1 (2.1)	
Pomacentrus fuscus		
dusky damselfish (S)	3 (6.3)	11 (35.5)
P. partitus bicolor damselfish (S)	18 (37.5)	24 (77.4)
P. variabilis cocoa damselfish (S)	20 (41.7)	27 (87.1)
Sphyraenidae		
Sphyraena barracuda		
great barracuda	11 (21.6)	11 (32.4)
Labridae		
Bodianus pulchellus		
spotfin hogfish (S)	8 (16.7)	29 (93.5)
B. rufus Spanish hogfish (S)	15 (31.3)	26 (83.9)
Clepticus parrae creole wrasse (S)		3 (9.7)
Halichoeres bivittatus		
slippery dick (S)	39 (81.3)	27 (87.1)
H. garnoti, yellowhead wrasse (S)	10 (20.8)	13 (41.9)
**Lachnolaimus maximus* hogfish (S)		24 (77.4)
Tautoga onitis tautog (N)	17 (35.4)	13 (41.9)
Thalassoma bifasciatum		
bluehead (S)	9 (18.8)	21 (67.7)
Scaridae		
Scarus spp. parrotfish (S)		11 (35.5)
Sparisoma viride		
stoplight parrotfish (S)		2 (6.5)
Sparisoma sp. parrotfish (S)		11 (35.5)
Blenniidae		
Hypleurochilus geminatus		
crested blenny (S)	2 (4.2)	
Parablennius marmoreus		
seaweed blenny (S)	19 (47.1)	7 (32.4)
Gobiidae		
Coryphopterus punctipectorphorus		
spotted goby (S)	14 (29.2)	5 (16.1)
Gobiosoma oceanops		
neon goby (S)	2 (4.2)	2 (6.5)
Gobiosoma spp. goby (S)		2 (6.5)
Ioglossus calliurus blue goby (S)	9 (18.8)	11 (35.5)
Acanthuridae		
Acanthurus bahianus		
ocean surgeon (S)	4 (8.3)	9 (29.0)
A. chirurgus doctorfish (S)		21 (67.7)
A. coeruleus blue tang (S)	2 (4.2)	17 (54.8)
Scombridae		
**Euthynnus alletteratus* little tunny	3 (6.3)	
**Scomberomorus cavalla*		
king mackerel	10 (20.8)	1 (3.2)
Balistidae		
Aluterus scriptus		
scrawled filefish (S)		1 (3.2)
**Balistes capriscus*		
gray triggerfish (S)	18 (37.5)	13 (41.9)
Monacanthus hispidus		
planehead filefish (S)	28 (58.3)	29 (93.5)
Ostraciidae		
Lactophrys spp. boxfish (S)		1 (3.2)
Tetraodontidae		
Canthigaster rostrata		
sharpnose puffer (S)	1 (2.1)	3 (9.7)
Diodon sp. puffer (S)	1 (2.1)	
Sphoeroides maculatus		
northern puffer (N)	2 (4.2)	1 (3.2)
S. spengleri bandtail puffer (S)	3 (6.3)	22 (71.0)
Molidae		
Mola mola ocean sunfish	2 (4.2)	
Sponge		
Nepheliospongiidae		
Xestospongia muta		
basket sponge		X[e]
Summary data		
Total species	85	96
Total families	34	38

a. An asterisk (*) indicates a target species (important in the recreational and commercial fisheries); S = tropical species; N = temperate species; species without a symbol designation (e.g., sharks, jacks, mackerels, etc.) were not the main concern of this study.

b. Some totals differ from the published study (Parker 1990) because three stations were eliminated for locality comparison, and counting errors were corrected.

c. Or *Paraconger caudilimbatus* margintail conger (S).

d. *Opsanus* spp. is probably an undescribed offshore form.

e. Although invertebrates were not usually recorded, the first observation of basket sponges was noted during our resurvey of the 210 Rock, and basket sponges were the subject of many underwater pictures and notations on cleaning stations throughout the second survey period.